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ABSTRACT OF THE THESIS

The History of the

Founder Effect in Anthropology

by

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Anthropology and Biology share an evolutionary paradigm. However, as Kuhn has argued (1970), this does not mean the paradigm is interpreted in the same manner. Nor does the sharing of an evolutionary paradigm automatically guarantee that rules abstracted from the paradigm by various sub-disciplines will be the same. Within anthropology, various other traditions of research (sociology, history) have contributed their own alternative rules and paradigms. These influences combine with the lingering pre-Darwinian paradigms (racism, polygenesim) to intermittently broaden the gap between the anthropological community understanding of the evolutionary paradigm and the biological community's respective understanding of the evolutionary paradigm. To examine this process, this thesis investigates the history of two, interlinked biological concepts, the "founder effect" and "genetic drift."

Introduction:

> The determination of shared paradigms is not, however, the determination of shared rules. That demands a second step and one of a somewhat different kind. When undertaking it, the historian must compare the community's paradigms with each other and with its current research reports. In doing so, his object is to discover what isolable elements, explicit or implicit, the members of the community may have abstracted from their more global paradigms and deployed as rules in their research. (Kuhn 1970:43)

Thirty years ago Thomas Kuhn argued that scientific concepts cannot exist in a vacuum. They reflect the intellectual and political climate in which they are found. At least three factors inform the manner in which scientific concepts are communicated. First there are the technical capabilities of the time, which limit most the types of knowledge obtainable from our physical world. Second there are the social norms that exist in every society and determine what kinds of knowledge are deemed valuable and productive. And last we have the disciplinary and intellectual traditions that govern the manner in which socially appropriate and technically feasible questions are framed and analyzed. The last factor is most relevant in interdisciplinary fields, such as anthropology, where traditions and approaches to the study of man have the potential to derive paradigms from various disciplines (biology, sociology). This is not to say that anthropology does not share an evolutionary paradigm with biology. Rather the rules that derive from such a paradigm have the greatest potential to diverge when disciplines do not share the same traditions.

Paradigms, as defined by Kuhn are essentially communal phenomena. Within the

sciences, they emerge as a consequence of the tension between two of the defining aspects of scientific communities. The first aspect is that of standardization. A paradigm is fundamentally a set of agreed upon assumptions and axioms describing proper questions to ask and the techniques by which answers are found (Kuhn 1970:10). If there are no mutually agreed to starting definitions, progress in the form of more extensive explanations of natural phenomena is very difficult to come by. Kuhn cited the varying theories on the nature of light and electricity prior to Isaac Newton and Benjamin Franklin's discoveries as prime examples of the effects a lack of consensus have on a scientific discipline (1970). However, this consensus must necessarily be limited, for the second aspect, novelty, to develop and sustain the general principles that underlie the paradigm. Kuhn referred to good paradigms as being "open-ended," (i.e. there are always more questions to be answered), an aspect which guarantees that the paradigm will continue to attract adherents even after the original, highly novel paradigm shift occurs (Kuhn 1970:10).

Kuhn maintained that paradigms are best demonstrated in textbooks (Kuhn 1970:47). They are structured to provide the student of the sciences with all the major discoveries, and axioms derived from them, as well as the conventionally-held interpretations of the original revolutionary achievements. The student is thus indoctrinated into the discipline, only to eventually question its very tenets upon reaching scientific maturity. Paradigms are ultimately guided by the questions asked by the master scientist, not the rules learned by the apprentice. Nonetheless, as noted in the quote above, rules are important elements of the study of paradigms, especially when paradigms are

shared across disciplines. Kuhn also identified paradigms across different levels of a discipline, noting that paradigm shifts can affect "only the members of a professional subdiscipline" (Kuhn 1970:49). Also, "rules" should not be conflated with paradigms, since although derived from paradigms, they are "usually common to a very broad scientific group" which may not completely share the same paradigm (Kuhn 1970:19).

To help illustrate how "rules" can diverge from paradigm, it is helpful to alternatively define it. A rule in this sense derives from a concept, and for illustrative purposes, can be thought of to a limited degree as a *meme.* Using Dawkins' definition, *memes* are:

> ...tunes, ideas...(that)...propagate themselves in the meme pool by leaping from brain to brain via a process which, in the broad sense, can be called imitation. If a scientist hears or reads about a good idea, he passes it on to his colleagues and students. He mentions it in his articles and his lectures (Dawkins 1989:192).

We can begin to understand how rules derived from paradigms can potentially diverge as they are translated across boundaries. As *memes*, the "founder effect" and its corollary, "genetic drift," are concepts that provide excellent examples of the subtle reshaping ideas undergo when they are translated across academic disciplines and cast in new light by technical advances. The degree of change and incorporation within other ideas, such as neutral evolution, reflect a combination of social forces, differing disciplinary traditions, and historically recurring debates that potentially undermine its proper interpretation and application. In this process, aspects of concepts can be lost. To identify if and when this has happened, this thesis shall attempt to trace the conceptual lineage of "the founder effect" from original observations in the latter part of the nineteenth century to the latest

observations in the twenty-first across the disciplines of biology, genetics, and anthropology. The incorporation of the concept into modern analytical models of human biological and cultural differentiation will also be discussed; as will the historical shifts in the meaning of the "founder effect," and the impact these shifts have on the current models of human biological and cultural differentiation.

Since the "founder effect" or as originally defined by Mayr (1942) the "founder principle," is our starting point, a comparison should be made between it and the larger concept of "random drift." This is an important distinction made by the authors of both theories, and hence should be illustrated prior to our analysis. After presenting them, I shall analyze the broad trends of citations of "the founder effect" and "genetic drift" within a representative sample of biological and anthropological journals for any indications of shared paradigms. However, first we should review some definitions of the terms we are interested in. Mayr's original definition of the "founder principle" describes:

> The reduced variability of small populations is not always due to accidental gene loss, but sometimes to the fact that the entire population was started by a single pair or by a single fertilized female, these 'founders' of the population carried with them only a small proportion of the variability of the parent population (1942:237)

This definition emerges directly from first hand observations of divergent reef heron color patterns in isolated Polynesian populations, and thus has a somewhat different context than Sewall Wright's 1931 mathematical definition of drift (whom Mayr acknowledges as paving the way for his definition of the founder principle) (Mayr 1942:237).

Wright's 1930 definition of drift describes how the process operates and it's relation to selection, population size, and migration:

> If the population is not too large, the effects of random sampling of gametes in each generation brings about a random drifting of the gene frequencies about their mean positions of equilibrium...If the population is too small, this random drifting about leads inevitably to fixation of one or the other allelomorph, loss of variance, and degeneration. (Wright 1930:354-355)

This is the manner in which Wright's definition is usually applied by anthropologists, however, the definition includes a significant aspect, selection, that affects the parameters required for "random drift":

> At a certain intermediate size of population, however (relative to prevailing mutation and selection rates), there will be a continuous kaleidoscopic shifting of the prevailing gene combinations, not adaptive itself, but providing an opportunity...for new adaptive combinations of types which would never be reached by a direct selection process (Wright 1930:354-355).

The central point made by Wright is that the process of "random drift" is inherent in every population that reproduces through combination of gametes. But it's relevance to populations relies on strict population controls as well as mutation and selection rates. At intermediate population levels, where the selection variable (s) is greater than the inverse of twice the population size (n), selection overpowers random drift through the differential survival and spread of favourable gene combinations. However, as Sewall Wright demonstrated in the 1929 article "The Evolution of Dominance," as (n) decreases, selection must increase to continue dominating gene frequencies. Hence, there is a point ($s<1/2n$)

"below which selection is not effective" (Wright 1929:559-560). Nonetheless there are two aspects to the concept which must be included, the randomness inherent below a certain point, and selection, which resumes its role upon an increase in population size. Both aspects are reiterated in concepts when defined by their authors, but as we shall see, they may be lost over time.

A cursory examination of the statistical trends in articles incorporating genetic drift versus "the founder effect/principle" suggests that on the whole, genetic drift has proved the more prevalent interpretation of unusually consistent gene frequencies. As Kuhn noted however, the same concepts can become different rules in different communities, hence we must analyze their interpretation across communal boundaries. In the table and graph immediately below, data on the number of articles citing the "founder effect/principle" versus articles citing genetic drift are shown.

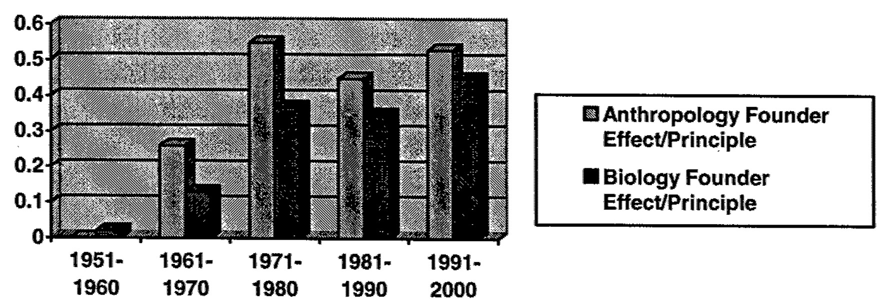
Founder Effect/Principle Citations in Biological Literature (by percentage of total articles published per decade)	1st column %
1951-1960	.02
1961-1970	.13
1971-1980	.37
1981-1990	.35
1991-2000	.45
Genetic Drift Citations in Biological Literature (by percentage of total articles published per decade)	**2nd column %**
1951-1960	.50
1961-1970	.55
1971-1980	.87
1981-1990	1.3
1991-2000	1.8
Sample size: 28 journals[I] from: http://www.jstor.org/search	

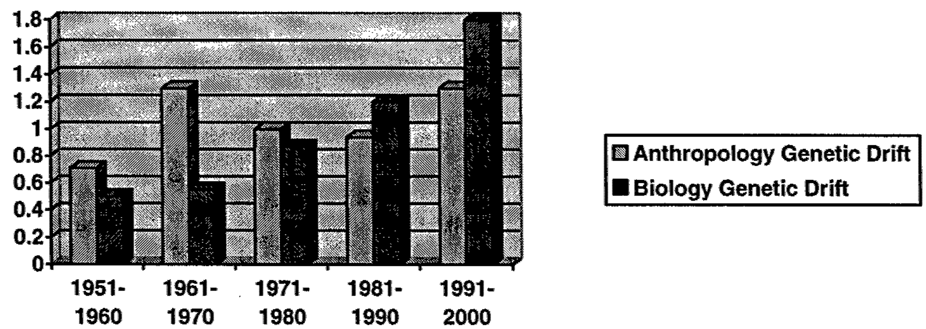
For biological journals, the relative proportions of citations indicate that "genetic drift" and "founder effect" citations have been present in generally less than one percent of the

journals surveyed. Nonetheless, there has been a steady increase in citations over the past fifty years, and throughout the span, "genetic drift" has proven the more popular concept in the literature.

Founder Effect/Principle Citations in Anthropological Literature (by percentage of total articles published per decade)	1st column
1951-1960	0
1961-1970	.26
1971-1980	.55
1981-1990	.45
1991-2000	.53
Genetic Drift Citations in Anthropological Literature	2nd column %
1951-1960	.71
1961-1970	1.3
1971-1980	1.1
1981-1990	.94
1991-2000	1.3
Sample size: 21 journals[II] from: http://www.jstor.org/search	

For anthropological journals, we see a similar dearth of interest in the concept, although it is interesting to note the same scale and rate of increase of interest found in biological journals. What is even more significant however, is the close agreement between the rates of increase.





The data represented on the table and chart is intended to graphically illustrate the "shared paradigm" referenced earlier. In both disciplines, relative proportions of "genetic drift" and "founder effect" citations increase, for most decades, in tandem from 1951-2000. During the 1950's and 1960's however, there is a reversal of relative emphasis. Anthropological journals cite "genetic drift" in twice the proportion of biological journals of the same time period. Thus it appears that during certain periods, relative interest in the "genetic drift" concept, as a subset of the evolutionary paradigm, may markedly diverge from the normal pattern. To understand the causes for this reversal, and degree to which the shared paradigm resulted in shared abstractions of "rules," a lineage of the "random drift" and "founder principle" concepts must be presented.

Chapter 1.

Pre-1900s. Observations of Variation and Isolation.

The concepts describing the "founder effect" have a long history within evolutionary biology, despite the term's traditional association with Ernst Mayr's introduction of the "founder principle" in 1942 for "...cases in which isolated populations of polymorphic species have a much reduced variation" (237). Indirectly, J.T. Gulick (1872, 1889, 1890, 1905), a missionary working in Hawaii, was actually the first to identify "...the divergent selection of recently isolated breeding groups" and speculate on the causes for such divergence (Beatty, 1999: 276). Gulick recognized one way to explain the differences in two isolated populations was to assume they were divided without regard to heritable variations within the original parent population (Gulick, 1872). Gulick derived this observation after realizing he was unable to see natural selection's operation in the variation of over two hundred species of the snail Family, *Achatnellidae*, on the Hawaiian island of Oahu.

Gulick himself put it best, noting "It is evident that when separated sections are small there is more likely to be diversity in the average characteristic of the sections and that roughly stated, the probabilities of divergence from this cause will be in direct proportion to the variableness of the species and in inverse proportion to the size of the different sections (1889, 1905: 186). In this statement, Gulick not only relates size and separateness to variation, he identifies the inverse relationship between the size of the separated population and the degree of variation it displays.

While Gulick, like Darwin, was unaware of the genetics underlying the process by which random drift operates on populations, he nonetheless identified the fundamental aspects of the relationship underlying random drift and hence, the "founder effect" as it would be later articulated by Mayr.

Biological anthropology during this period proceeded along a somewhat different tract than biological research, despite the shared Darwinian paradigm. Penniman (1965) notes that it was in fact Social Darwinism that had the greatest impact on theories of the biological nature of man (74). This is not entirely surprising, as the roots of this paradigm are both extensive and deep. The earliest attempts at racial classification can be ascribed to Francois Bernier's 1684 racial classification of Europeans, Lapps, Asiatics and Africans (Slotkin 1965: x). This classification, in turn provided the basis for Linnaeus (1735) and Blumenbach (1865) who essentially developed the foundation for modern racial classifications. Linnaeus's 1735 classifications of *Homo* into distinct but broad varieties: *Europaeus albus*, *Americanus rubescans*, *Asiaticus fuscus*, and *Africanus niger*, are also reflective of the social interpretations of racial differences: *Europaeus* was described as "white, sanguine, muscular" with "hair flowing, long. Eyes blue" and "Gentle, acute, inventive" and most importantly, "Governed by laws" (Slotkin 1965:178). While *Afer* (Africans) were described as "black, phlegmatic, relaxed" with "Hair black, frizzled. Skin silky," African women were "without shame" while all Africans were "Crafty, indolent, negligent" and "Governed by caprice" (Slotkin 1965:178).

Differences among people were interpreted in accordance with everyday

observations on nutrition and development, in accordance with the biblical principle of monogenesis, the belief that all humans descended from Adam and Eve. Differing degrees of development then, along with inheritance of acquired characteristics, could be used to explain human variation. As Linnaeus (1735) states in his attempt to explain the physical differences of Laplanders from the rest of Finland "If we give a young puppy plenty of food, he will grow large; if but little, he will turn out small...If kept warm, he will also grow to a much larger size than if he is always inured to cold. The same remarks may be applied to the people in question" (Slotkin 1965:178). This theory was rectified by Linnaeus (1735) with the monogenesis dogma with a very interesting conclusion, "I have a notion that Adam and Eve were giants, and that mankind from one generation to another, owing to poverty and other causes, diminished in size. Hence perhaps the diminutive stature of the Laplanders" (Slotkin 1965:178).

Directly related to the question of racial variation, the theory of polygenesis arose. It first appeared in the twelfth century, proposed by an Italian scholar, Gillaume de Conches (Slotkin 1965: x). His position was maintained, with little change, by Paracelsus and Giordane Bruno during the sixteenth century despite Leonardo Da Vinci's indirect support during the fifteenth (Da Vinci criticized the monogenesis attempt to account for racial variation through the geographic differences in inheritance of acquired characteristics) (Slotkin 1965:x). The popularity of polygenesis theory would not peak until the seventeenth century, after the 1655 publishing of Isaac de La Peyrere's exposition, yet would remain as an essential counterpoint to the orthodoxy of monogenesis. Even during

the 19th century, unfortunately, the fossil record was still not sufficient to produce a standard interpretation of humanity's evolution and proofs were often derived through comparative analysis of modern human beings and modern apes. The result was a preoccupation with finding a "missing link" exactly half way between modern apes and modern man (Penniman 1965:74). These contrasting viewpoints, single origin vs. multiple origins, are of almost timeless antiquity. They likewise continue to influence the debate over the origin of humans and their differentiation. As I shall demonstrate, the evolutionary paradigm shared by anthropologists and biologists must contend with these earlier notions, and is often unsuccessful in standardizing the evolutionary paradigm and the abstractions of rules governing the study of humans.

This trend is even more evident in socio-cultural anthropology. Penniman has suggested that directly after Darwin's 1871 publication of the Descent of Man, social anthropologists and sociologists were quick to apply Darwin's terms and concepts, "while still clinging to old ideas which are the result of the mechanical revolution" (1965:74). The result were ideas that one nation conquers another because it is superior or that someone who lives easier and profits more from their work does so because they are "fitter to survive" (Penniman 1965:74). Penniman suggests that these ideas are indicative of a blending of the terminology of Darwin with the pre-Darwinian notion of the "competition for mechanical efficiency" (Penniman 1965:74). From this premise, Thomas Huxley and Herbert Spencer described society as an organism, with internally warring elements that varied in their "mechanical efficiency and progress" and hence led to "the strongest

surviving" (Penniman 1965:74). The Darwinian paradigm was thus distorted to justify class and racial differences by both the forces of Social Darwinism that emerged after the 1859 publication of the Origin of the Species, and the influence of the "mechanical revolution" before.

Chapter 2:

1900-1930 Genetics, Racism and the First Synthesis

The rediscovery in 1900 of Mendelian Genetics outlined the mechanism by which "random drift operates" and in the process sparked a 50 year period of "great turmoil in Evolutionary Biology" as leading Mendelian geneticists like Goldschmidt, De Vries, Bateson, and Johannsen rejected selection, favoring "saltationism" instead (Mayr 1999:xiii). From 1900-1915, the Mendelian geneticist's mathematical rendering of a population's genetic structure allowed radical reinterpretations of the forces underlying variation. Interestingly, even when the results of T.H. Morgan's experiments at Columbia on *Drosphila* indicated salationism could not account for observed genetic variation, selection was still ruled out by early Mendelians, who espoused a "modern" revision of orthogenesis (a Pre-Darwinian paradigm of internally-driven evolution) (Mayr 1999:xiii).

The community of biological scientists was effectively polarized on the issue of what underlies variation, and the extreme claims of the Mendelians and their successors the Neo-Darwinist forced a large number of their oppositely-oriented colleagues, the zoologists and botanists, into accepting an equally extreme view, that of Lamarckism. In the absence of consensus among biologists, the early anthropologists studying the extent and distribution of human variation (Manouvrier, Martin, Keith, Hrdlicka, Pearl, and E.A. Hooton) appear to have fallen back on an earlier assumption that human populations were "...unvarying and that their attributes were permanent" rather than apply either of the extremes represented in the debate (Leslie and Little 2003:29). The assumption of

biologically fixed-species drew partly from the eminent anatomist Ernst Haeckel's 1905 depiction of species (including man) on the great tree of life as fixed essences, but mostly from the social conditions of the time. Glaring racial differences in class and wealth continued to beg naturalistic interpretation from governments and institutions unwilling to address inequality and early anthropologists were still influenced by these social forces (Slotkin 1965:178-9, Caspari 2003:66-67).

Anthropologist's understanding of variation in an evolutionary frame was thus severely restricted by these two main factors during the early part of the twentieth century. On the one hand, the most progressive and arguably greatest anthropologist of the time, Franz Boas, had rejected "all aspects of evolutionary thought" in his noble goal of "the promotion of racial equality" (Armelagos and Van Gerven 2003:56). This rejection was not at heart scientific, but largely stemmed from ideological differences with the forces arrayed behind the cause of evolution as it applied to human beings. Opposed by Boas were the evolutionists L.H. Morgan and E.B. Tylor. Morgan and Tylor were not actually interested in describing the underlying process of human variation so much as placing racial categories on an evolutionary hierarchy.

Hence, Boas's outright refutation of their principles meant he never organized the variation he observed in immigrant skull morphology in 1912 into an evolutionary framework (Bee 1974:63). The result was that Boas's students were left with "few questions to ask beyond questions of diffusion, and few methods to apply beyond description" (Armelagos and Van Gerven 2003:56). Also opposed by Boas was Ales

Hrdlicka. Hrdlicka's laudable accomplishments, the 1907 systematic analysis of New World skeletal material, 1918 founding of both the *American Journal of Physical Anthropology* and the American Association of Physical Anthropologists, and 1920 identification of the "shovel-shaped incisor as a racial hallmark linking Asian and New World populations," were tainted by his steadfast conviction that race informed culture and that "Caucasian biology was the norm against which other races were to be compared." These beliefs signified the "racial typological approach" that conflated races with species. All of Hrdlicka's influence thus promoted the view that races were scientifically valid objects of study, inherently essential, although in reality they are geographically highly variable (Slotkin 1965:179, Armelagos and Van Gerven 2003:56).

This approach was most explicit in the inaugural issue of the *American Journal of Physical Anthropology* which stated: "The paramount scientific objective of physical anthropology is the gradual completion, in collaboration with the anatomist, the physiologist, and the chemist, of the study of the normal white man living under ordinary conditions" (Hrdlicka 1918:18). Clearly, there was disciplinary boundary crossing at the time, but the blinders imposed by social forces (racism) were far more restrictive than a lack of knowledge of other disciplines. Even the earliest genetic data derived from Leopold and Hirszfield's 1919 survey of ABO blood types among World War I recruits was used not to illustrate the inherent geographic variation over distance of genetic traits, rather it was used to construct racial typologies and classifications (Penniman 1965: 188-9, O'Rourke 2003: 102).

Despite Gulick, Mayr, Wright, and Fisher's observations, the concept of isolation and selection as producing substantial variation within a species was slow to filter from zoology to anthropology. Nowhere is this misunderstanding more evident than in the statements of E.A. Hooten whose impact on the first generation of physical anthropologists cannot be understated (seven of the first eight presidents[III] of the American Association of Physical Anthropologists were his students). Hooten, like Hrdlicka and others was so opposed to the idea that racial traits were not biologically fixed (and thus products of isolation and variation affecting all human groups) that he explained the presence of "Negroid" racial features in the New World as the result of "a minor infusion of Negroid blood" brought by "pseudo-Negroid" migrants across the Bering straits, all the way from Africa (Hooton 1930:356).

There seemed to be no perception of living populations undergoing continuous change and adaptation to their environment could arrive at the same morphologies. Instead, the typological paradigm in which they worked interpreted all intermediate or homologous structures as the result of interbreeding "between once-pure primary racial groups that relatively recently underwent a secondary race formation stage and then a tertiary stage—in each stage, hybrid races formed from the preexisting ones" (Caspari 2003:70). In their view, divergent characters must have been the result of hybridization, since their views on race were essentialist. Thus, the very concept of differing rates of gene flow (genetic drift) as a source of divergence was ignored, despite it's growing relevance in zoology and genetics, an oversight we can most likely attribute to the preoccupation of the time with

essential racial characters (Caspari 2003:71). To their credit, outside of their academic theories, Hooten and Hrdlicka thought of themselves as antiracist and joined Boas in his efforts to reform physical anthropology and move it away from racist foundations. Unfortunately, while they were certainly capable of criticizing the common racial stereotypes, they were unable to undertake the same critiques of their own typological paradigm. The biological determinism that typified the typological paradigm thus persisted in Hooten's students Stanley Garn and Carelton Coon who continued to write about the classification of races in essentialist, typological themes well into the 1950s.

In other areas of anthropology, notably cultural, there were however, notions of change in culture that were neither adaptive nor functional, but indicative of simple historical events. In essence, these concepts mirror the concept of "the founder effect" and consequently, "random drift." Although in typical fashion, they appear to have developed independently. I refer to the term "disappearance of the useful arts," as coined by W.H.R. Rivers in the 1926 publication Psychology and Ethnology. Rivers coined the term while attempting to account for the curious fact that on the Torres islands of Polynesia, the technical skill to manufacture a canoe had been completely lost, despite its timeless utility. Rivers surmised that simply losing the craftsmen who made canoes to chance events could account for the discrepancy by noting “It is only necessary for such a limited body of men to disappear either as the result of disease or war or through some natural catastrophe, to account for the disappearance of the art…(Rivers 1926:200). In River's description, the term "drift" is not used, nor "random." There is also no obvious connection with Wright's

1931 calculations[IV], as they had not been made yet. The position of this concept then, at least for biological anthropology is as a side branch on the lineage, not ancestral to "random drift."

In human paleontology, prior to the modern synthesis, the situation was no better than in biological anthropology. Most human paleontologists could only speak of a "poorly defined tendency towards progression within one or several lineages of higher primates" and while some had accepted the notion that humans were the products of natural selection, many did not. Still more did not consider the impact of selective pressure on humans to any great degree. However, by the late twenties and early thirties, things were beginning to change. Modern notions of adaptive radiation and selection for key human traits were beginning to develop and with the 1924 discovery of the savannah environment of the Taung child, *Australopithecus africanus*, (Dart:1925) the adaptive radiation hypothesis gained significant momentum. Unfortunately, wider application was still hamstrung by a single lineage (*Pithecanthropus*-Neandertal-Human) approach to human evolution which "enjoyed considerable popularity in academic circles for much of the 20th century" (Ward 2003:78).

Chapter 3: Race and Drift

1930s -1940s: A Modern Synthesis

Among biologists of the early 20th century, racial blinders also existed, but the focus on animal species and natural laws allowed more flexibility. Unlike the anthropologists who derived their biological foundation for a species from Haeckel (and subsequently operated in the socially charged field of human classification), biologists were free to investigate "natural laws." Thus from the beginning their paradigms were subtly different. To the early 20th century biologists it was well understood that species varied across their range. But since there was little consensus over how to classify them, the mechanism by which this variation persisted became an important area of research. The notion of "random drift" at this point was developed by Sewall Wright through a series of groundbreaking calculations[IV] (1931, 1932, 1935) modeling the gene flow of a species spread across a variable landscape. Wrights models showed that in partially isolated, peripheral segments of a populations (Fig 7D and E), the homogenizing effect of gene flow was lessened and stochastic effects would be amplified through "sampling error" (Wright

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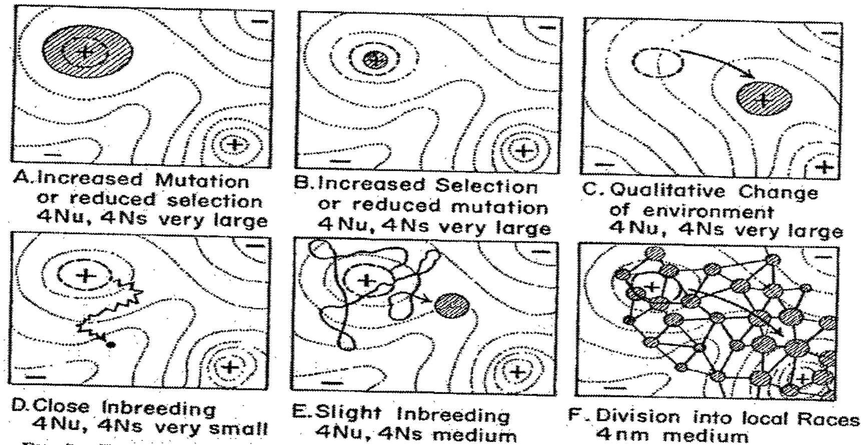


FIG. 7. Token representation of a portion of the multidimensional array of genotypes of a population with fitness contours. Field initially occupied indicated by crosshatched area (multiple subpopulations in F). Courses indicated in C, D, E and F by arrows. Effective population numbers, N (total), n (local); v (mutation), s (selection), m (migration) (from Wright, 1932, Fig. 4).

1932).

Although not linked to the "founder effect," essentially this process underlies the "founder effect" and has hence been interpreted as a subset of drift. During the 1930s and 1940s the newly articulated concept of "random drift" was thus being used to explain many cases of nonadaptive variation (Dobzhansky and Queal 1938; Diver 1940; Wright 1940). As with many new concepts however, it was frequently misapplied, as later research (Dobzhansky 1943; Wright and Dobzhansky 1946; Cain and Shepard 1950, 1954; Shepard 1951, 1952) revealed that many of the cases of apparently "nonadaptive" variation could be explained by natural selection (Beatty 1999). This first large scale attempt to model the gene flow underlying the naturally occurring variation across a species range demonstrated conclusively how the genetic structure of populations were dependent on geography in both an adaptive and non-adaptive sense. Unfortunately, the anthropologists of the 1930s, trained by Hooten, were not prepared socially or intellectually to think of the human species as being so genetically flexible. Accordingly, the role of simple geographic

isolation as a factor in divergence was completely overlooked until the 1950s.

However there were early disputes over the implications of Wright's calculations[IV], which may have also contributed to anthropologist's reliance on earlier concepts of species change. This disagreement (primarily with Fisher) led Wright to characterize the debate over the frequency of speciation during this period due to sampling error as "...a question of the relative values of certain coefficients" (1948, p291). In principle however, most Wright's of contemporaries (including Wright himself) firmly believed that selection guided the ultimate form derived from the variation imposed by isolation. This distinction however, became lost as the debate became more polemical, and prompted Wright to author one of his last articles in 1982, summarizing the history of his concept.

He identified the origin of the debate with the publishing of his rival R.A. Fisher's 1930 synthesis, The Genetical Theory of Natural Selection. Fisher's goal in publishing the book was to "...bring all evolution under a single simple formula, his 'fundamental theorem of selection,' the rate of increase in fitness of any organism at any time is equal to its additive genetic variance in fitness at that time" (Wright 1982:429). The Fisherian synthesis is significant for two of its accomplishments. First it solved the problem of how species adapt genetically to their environment by summarizing Wright's (1931), Fisher's (1930), and Haldane's (1932) calculations on the rates at which genes with a small selective advantage quickly establish themselves in populations. Second, by demonstrating this mechanism it established a definition of evolution that geneticists could universally agree on, the change in gene frequencies over time (Wright 1982:429).

However, in Fisher's promotion of the role of selection that this model espoused, Wright believes his views on the role of isolation were overemphasized and his calculations misrepresented as promoting the role of "random drift" as *the central force* in variation (Wright 1948:280). Wright however, claimed nothing could be further from the truth, and that his models always demonstrated "random drift" as a special case, not indicative of the vast majority of speciation events, and still secondary to natural selection in determining the final form of a species. But by polarizing the issue of random drift versus selection, Wright's work came to be identified primarily with *nonselective* interpretations of variation. Wright himself summarizes the impact of this characterization on biology:

> In spite of this, most authors, Huxley (1942) and Fisher and Ford (1947) followed by many others (including textbooks published in 1979 and 1980 have attributed to me the view that fixation of nonadaptive characters by random drift was the essence of my theory (Wright 1982:434).

Accordingly, when Wright is now cited (by anthropologists and geneticists alike) it is usually to demonstrate a case of apparently "nonadaptive" variation, although Wright repeatedly stressed the special conditions under which it occurred and the need to rule out selective forces. As I shall demonstrate later, anthropologists who draw on Wright's work during the 1960s and 70s, frequently miss this distinction as well and hence fail to rule out selective forces before deploying the "random drift" rule. This indicates a loss of the "directional" aspect of the "genetic drift" concept and is exactly what Kuhn warned about in the interaction of shared paradigms, a case of abstraction of a rule without complete

understanding of the "Modern Synthesis" paradigm from which it is derived.

By the time of the true "Modern Synthesis" however, there was still a great rift within biology. Although geneticists and general biologist had agreed on a genetic basis for adaptation and evolution, the zoologists and botanists still favored Lamarckism (Mayr 1942. This belief stemmed from their conviction that geneticists had not solved the central problem, demonstrating how the genetic basis translated into phenotypically novel species. By translating genetics into phenotypical variation in his 1937 book Genetics and the Origin of Species Theodosius Dobzhansky not only explained the genetics of selection and drift in the origin of species, but did so in the language of a taxonomist, and effort which brought zoologists and botanists back into the fold of evolutionary biology. Thus when Mayr compiled his observations on variation and the science of taxonomy into the 1942 edition of Systematics and the Origin of Species From the Viewpoint of a Zoologist he draws on both the calculations of Wright and the synthesis of Dobzhansky to articulate the "founder principle." Interestingly however, and probably signifying his unease with the non-selectionist characterization Wright received, Mayr then and now "does not consider the founder effect to be an instance of random drift" (Beatty 1999, p276).

For Mayr, the definition of the "founder effect" implied simply that at some point an original breeding population was extremely small, greatly reducing genetic variation. In this manner the "founder effect" is an explanation for apparent genetic homogeneity in populations living under conditions which promoted isolation and divergence from the parent population. To emphasize the selective aspects of the "founder effect," Mayr later

notes that isolation upsets the epistatic interaction (in which replacement of one gene normally requires adjustments at other loci) that normally balances genotype frequencies (2001:127). Mayr extrapolated that this "freeing up" of available genotypes can account for the "widely divergent phenotypes" that characterized some "founder populations" (2001:127). Also, Mayr reiterates Wright's emphasis on the extreme conditions under which the "founder effect" is possible by noting that founder populations are most relevant when "...established by offspring of a single fertilized female or by a few founders" (1942: 237).

For human paleontologists of the 1940s and 50s, these discoveries were gradually, though irregularly also filtering across the disciplines. Franz Weidenreich for example, the mentor of the current Multiregional Theory author Milford Wolpoff, held that "The development and stability of...constitutional types and their occurrence in all racial groups of mankind today...give evidence that geographical isolation is not and cannot have been a prerequisite for the establishment of (differentiations) in man (1943a:249-250). This viewpoint is also found in Howells(1942), where he notes "The great majority of racial features are obviously not adaptational, and consequently bespeak a more or less random fixation of random variations of color and details of shape, in different groups of *Homo sapiens* which attained a relative isolation" (191). As I shall demonstrate later, these essential misinterpretations of the relationship between isolation, random drift, and adaptation filter down into the current Multiregional Model. For now however, it is sufficient to state that principles outlined by Mayr and Wright were understood in varying

ways by human paleontologists at the time, and their interpretations were largely reflective of whatever model the author wanted to promote, rather than the genuine principles as described by Wright and Mayr.

This uneven distribution of understanding was indicative of the recent upheavals in the human paleontological paradigm. The former paradigm, which arbitrarily divided all human-like fossils into "ancient" and "modern" categories, reflected a bias towards cranial size as the paramount feature of human ancestors. Thus, the "Piltdown Man" hoax (with it's "modern" skull and filed down orangutan jaw), and "Galley Hill Man" (a modern skeleton inaccurately dated to the Middle Pleistocene) became standards for human ancestors. S.L. Washburn remarks that from "1915-1940 the most common arrangement of fossil men...postulated that there had been two separate evolutions in the Pleistocene, one of the ancient forms of man...and one of the anatomically modern forms" and thus every fossil cranium that appeared slightly primitive was classified as "ancient" (Brew 1968:102). Since all of these fossils were recovered from England, (proving the English were descended from the first modern humans) social forces of racism and nationalism also help explain the persistence of the Piltdown hoax in England, which was not popularly debunked until 1953 by J.S. Weiner, K.P. Oakley and W.E. Le Gros Clark in the *Bulletin of The British Museum* (Washburn 1953:762). During this period of profound embarrassment for the human paleontological paradigm, Dobzhansky (1944), Mayr (1950, 63) and Simpson (1963) were thus able to exert profound influence, and shift the paradigm from its typological roots of "fixity and antiquity" to the modern synthesis (Penniman 1965:202).

Chapter 4.

1950s: The New Physical Anthropology meets Mendelian Genetics

For biological anthropologists of the 1950s, the net effect of the "Modern Synthesis" of selection and genetics into a Darwinian framework resulted in a renewed emphasis on selection and gene flow that incorporated the ideas of Mayr and other biologists investigating "ecogeographical rules." On the genetic level however, the initial attempts at this stage were less rigorous or impressive. C.B. Davenports (1945) study of "cross cultural dietary differences and mobility patterns as a result of underlying genetic differences between populations" underscores an initially poor abstraction of the principles outlined by the modern synthesis (O'Rourke 2003:101).

The first genuine opportunity for cross-discipline consensus on the shared paradigms of Evolutionary Biology and Anthropology came with the Cold Spring Harbor Symposium of 1950. The interaction of geneticists, physical anthropologists, and biologists resulted in "The New Physical Anthropology," published in the *Transactions of the New York Academy of Sciences*, and a paradigm shift from typology to:

> -the study of populations, not races
> - the study of human variation, not typology
> - a shift to design and hypothesis testing rather than descriptive studies
> - a new foundation of evolution and adaptation (Washburn 1951).

The establishment of a consensus among biologists and anthropologists evident in the "New Physical Anthropology" was not without its difficulties however. Mayr, for example,

presented at the symposium a paper on "Taxonomic Categories in Fossil Hominids" that severely criticized the typological approach still being used by some paleoanthropologists.

With the dismissal of the typological approach, a new grounding of the race concept in evolution and adaptation was required. Race was subsequently shifted away from an essential, biologically determinist viewpoint, into a flexible, ecologically dependent indicator of partial isolation by selection and geography. In key articles that followed, notably J.B. Birdsell's "Some Implications of the Genetical Concept of Race in Terms of Spatial Analysis" (which was a direct result of his attendance at the symposium) and G.W. Lasker's "Mixture and Genetic Drift in Ongoing Human Evolution," notions of "fixed racial characters" are thoroughly absent (1952). In their place is an emphasis on the four factors of evolution, "mutation, selection, mixture and drift" of which two in particular, drift and admixture, are discussed as opposed forces in a small apparently isolated population (Lasker 1952:433).

Birdsell (1951) however, focused his work on the interdependency of selection, isolation, and population size as displayed in the pattern of gene frequencies among Western Australian Aborigine tribal groups. This is contrasted to Lasker's research, in which the questionable notion of "mixture" between races is the primary focus. While Lasker did cite Wright's observation that "if the species is divided into genetically isolated subgroups drift will be especially important," he still abstracted a rule from the earlier paradigm of focus on "purity" of groups (Lasker 1952:433). This emphasis is best evidenced by Lasker's statement:

> The present paper is concerned with an effort to estimate the roles of two of these factors, drift and mixture, in certain specific contemporary situations and to assess their relative importance...This in no way contradicts the assumption that there must have been a time in the past—during the period of establishment of the racial differences which are now observable—when breeding groups were smaller or more endogamous" (1952:433, 436).

The qualification that in the past racial groups were more pure is a relict of the earlier notions of fixity. Simply applying the principle of uniformitarianism would have been the most parsimonious statement to make, and more in accordance with the calculations made by Wright. In this case, it appears that while the basic paradigm of heredity was still being established, it had not yet completely overturned the abstracted rule of fixity in times past (Kuhn 1970:18-19). The difference between Lasker and Birdsell's interpretations (Birdsell's interpretation of the Aborigine data was grounded in evolutionary history) may lie in the attendance by Birdsell at the symposium and his interaction with the leading biologists of the time. In his case, the opportunity for standardizing the shared paradigm would have been much greater.

This is not to say that Lasker did not understand the concepts of genetic drift and isolation, rather because of his faulty abstraction of fixity, he simply did not apply the notion of drift backwards in time. He certainly applied it to the future, noting "In general, man is apparently now in a period of genetic amalgamation. The high rates of admixture probably prevent wide local variation to develop by drift..." (Lasker 1952:436). This statement also underscores another faulty abstraction. Outside of the second paragraph,

Lasker does not mention selection or mutation as factors which could account for high gene frequencies in partially isolated communities. One explanation for this discrepancy is his reliance on Wright's calculations, and the possibility that he derived his interpretation of Wright's theories from the nonselectionist characterization made by Fisher. In Birdsell's case, Dobzhansky (1957) was the stronger influence, whose emphasis on selection and drift acting in concert, prompted Birdsell to later quip "Drift pulls the trigger and selective forces then come into action to create a new level of equilibrium in the gene pool" (414: 1972). Lasker's article, in all fairness however, was clearly focused on the mathematical functionality of the drift concept. However, as I shall demonstrate, this early simplification of the "random drift" concept into an approach for analyzing human demography is a significant milestone for later research.

Other anthropologists studying the extent and pattern of human variation also displayed inconsistent application of the principles of isolation and distance that underlie the "founder effect" and random drift. This is despite the fact that by 1950 most anthropologists were no longer concerned with identifying the biological features that typified the "races" of man. Instead, thanks to Mayr (1950) and Dobzhansky(1944), the focus shifted to considering man a polytypic species with geographical subdivisions (Garn and Coon 1955:996). What remained to be agreed upon, and is indicative of the delayed abstraction of the new taxonomy publicized by Mayr (1942), is how many races of man there were. Some still preferred to go by similar characters without considering the evolutionary origin or geographic separation of races. Others, such as Coon, applied the

new biological species concept outlined by Mayr (1942) and concluded that all the variations could be reduced to falling within one of two categories, geographic races and local or microgeographical races. While Garn and Coon's definition is certainly more up-to-date at this point than many of their contemporaries, and indicates a modern understanding of the process of drift and isolation in producing regional differentiation, it is in their definition of local races that we see the first inkling of a faulty rule abstraction:

> ...the populations called local races...are units that can change most in evolutionary time. In many cases such local races can be identified not so much by average differences, but by their nearly complete isolation (Garn and Coon 1955:997).

Australian aborigines, Kalahari bushmen, and the Ainu are suggested as "rather isolated, small, and scattered populations" and lumped together with Pitcairn Islanders and the inhabitants of Tristan de Cunha as "happily breeding and effectively isolated local races" (Garn and Coon 1955:998-999). The conclusions that necessarily flow from these assumptions are that such populations are ideal candidates for "the founder effect" and random drift, since they are assumed to be isolated despite the fact that no direct historical evidence (except for the islanders) conclusively demonstrated them to be so.

The proof of these assertions lies in the following statement made by Garn and Coon; "Local or microgeographical races, isolated by distance or by numbers and corresponding more nearly to Mendelian populations" are "...not only are susceptible to direct study but also afford insight into evolutionary mechanisms still at work in shaping man" (1955:1000). Clearly, Garn and Coon, like Lasker, hastily assumed these populations

were under essentially laboratory conditions for the same purpose, to predict the evolutionary future of man. This traditional difference with biology (which sought to understand the process in principle) again led to a faulty abstraction of the rules regarding random drift and "the founder effect." Wright and Mayr's examples of isolation were far more lacking in gene flow than the Kalahari Bushmen or Ainu, and the relative sizes were also much smaller than the local populations of indigenous peoples. Furthermore, the degrees of selection, both natural and sexual, were integral parts of those theories, and were completely left out of these early applications of the "founder effect" and random drift concepts.

Chapter 5:

1960s. The Slow Death of Biological Determinism

By the 1960s, the stage was being set for a radical reinterpretation of variation. In the early part of the decade however, the changes in the concepts of random drift and "founder effect" were largely aimed at refining and drawing distinctions between the two. Like the Cold Springs Harbor Symposium of the previous decade, an event that publicized and standardized interpretations of biological concepts was the 1960 University of Chicago Centennial Conference on "Evolution After Darwin." During the conference two panels, the second and the fifth directly addressed concepts of isolation, random drift, and human evolution. In the second panel, Sewall Wright, Ernst Mayr, and Theodosius Dobzhansky discussed the balance and interaction of natural selection and "other agencies such as random drift" in the direction of evolution (Tax and Callendar 1960:108). On this topic Wright notes that "modern geneticists" are in full agreement that interaction between random drift and natural selection underlies variation, with natural selection as a "guiding principle." In Wright's summary of the process of drift he states unequivocally that local populations "largely, but not completely isolated...inevitably drift apart in genetic constitutions, partly under the influence of differences in local conditions and partly from random processes" (Tax and Callendar 1960:117-118).

Despite Wright's insistence that drift requires a *high* degree of isolation and the need to consider selection by environmental differences, the approach to clinal genetic analysis discussed by Newman in the article entitled "Geographic and Microgeographic

Races" clearly demonstrates that while some aspects of drift were understood, the important points were still lacking (1963: 191). The central point of Newman's article is to break down the old typological category of race and replace it with Rensch's (1929) idea of the "local or micro race as an approach to a Mendelian population" (Newman 1963:189). Newman disagrees with the 1955 taxonomic efforts of Garn and Coon on the basis of their lack of biological characteristics, and criticizes the brief serological justifications underlying Garn's 1961 grouping of nine "races." Instead Newman offers his own, more biological foundation of a geographical race as "characterized by a number of genetically controlled traits that are geographically associated throughout its range" and cites the work of a zoologist, Brown (1958), to support his approach.

Unfortunately, Newman's approach, while more biologically grounded than Garn and Coon's, fails to abstract the most current ideas about gene flow, distance, and random drift that were in circulation at the time. His confusion results from a continued reliance on phenotypic traits, evidenced by clines, as markers of population history. Comparing the ranges over which the broad geographic races spread, Newman derives a "general principle that when a geographical race extends over a wide climatic range, it may be strongly cross-clined by the traits following the ecological rules" (Newman 1963:190). In essence, Newman applies the geographic race concept to the ecogeographical rules (which do reflect drift and selection) without questioning whether the geographical race concept at the scale they were using was even a valid starting point. By adopting it as his frame, he concluded that geographic races with the most "cross-clines" (variability in phenotypic traits) have a

longer population history. It appears that while Newman seemed to understand that distance allowed variation to flourish and selection guided the variation, he did not incorporate any aspect of population size as a factor in accelerating divergence and geographic variation. His conclusion is correct in noting that variation requires time, but he did not seem to realize that variation can also develop quickly in smaller, isolated population. This alternative hypothesis would have led him to consider that a clear correlation between variation and time was not always correct, and hence an African origin for humanity, a possibility.

The conclusion Newman reached may have also been influenced by a misunderstanding of the fossil record as well. Newman frequently cites Carelton Coon and Stanley Garn extensively, both of whom were still theorizing in the typological, polygenist mode. Hence, Newman believed that neandertal evidence meant that Europe, not Africa, had the longest fossil record of the *Homo* genus and was hence the origin of humanity. This fact justified his faulty interpretation of cross clines: since to him, "the European geographical has perhaps the longest known fossil history...and is strongly cross-clined" (Newman 1963:190). On that basis, African and other Old World populations were interpreted as entering their lands only during the Neolithic, a late arrival which did not provide enough time for the cross-clines to develop. These conclusions were further bolstered by the early genetic data on blood groups that portrayed Africans as inhabiting one of the "serologically...most distinctive areas of the world" and displaying an "essential genetic similarity...despite their morphological and cultural differences" the inherent

contradiction between phenotypic variation and genetic similarity was completely overlooked.

Newman's explanation for this similarity is that African populations are recent, and that the Sahara has isolated them from interbreeding with the older European populations. Neither natural selection, nor migration, were explicitly ruled out as factors influencing blood type frequencies. Instead the conclusion reached by "Combining phenotypic and genotypic data" was that "the African, Asian, and Amerindian geographical races show considerable distinctiveness of traits and good association of a number of them" (Newman 1963:191). Newman's reasoning for this approach is best indicated by his own words, clearly echoing Lasker (1952) and Garn (1955): "Quite aside from its application to actual data, one can hardly quarrel with the concept of local or micro-races as Mendelian or demographic populations" (Newman 1963:192).

Thus even though Dobzhansky's Genetics and The Origin of Species (1957) is referenced as a source, as are Julien Huxley's The New Systematics (1940), and Mayr's article on the genetic basis of species in *Advances in Genetics* (1948), the inherent interplay of natural selection and random drift was seemingly ignored to bolster the geographic race concept. Not surprisingly, Newman's article prompted a response from Dobzhansky himself who reemphasized that "race boundaries" are only sharply drawn "between island populations" (Dobzhansky 1962, in Newman 1963:196). Furthermore, Dobzhansky also reemphasized the importance of ruling out selection, in this case sexual selection, by noting that when investigating human blood antigens:

> ...the distribution of a certain gene, or a certain category of genes (e.g. those for blood antigens)...we must not forget for a moment that human cultural differentiation had made the biological differentiation of the human species far more complex. Consider, for example, the populations of India, genetically dismembered by more than two millennia of the caste system (1963:196)

Dobzhanksy's critical point is that Newman's assumption that human populations follow Mendelian rules of random mating (i.e selection, migration and mutation are ruled out) is inherently fallacious and describes little of the distribution of human variation.

Newman was by no means the only anthropologist to mis-abstract the rule of isolation as it relates to geographic race formation. No anthropologist during the sixties has probably received more criticism for their implicit racist and segregationist views than Carleton Coon. To a degree, the worst characterizations are unfair. Reviewing his 1963 The Origin of Races, his views on the source of morphological variation in Africa still reflect biological essentialism of races, but these views do not preclude his postulating that Africa is perhaps the source of mankind. For an apparently avowed racist, this would amount to heresy. His scientific understanding of the conventional definition of drift is the most interesting however:

> Gene frequencies, then, change more rapidly in small rather than in large populations. The process by which such fortuitous changes become major characteristics of populations is called genetic drift, or the Sewall Wright Effect, after its discoverer. (Coon 1963:48)

Coon clearly cites and understands Wright's definition of the process, but does he understand the context as well? It appears so, as Coon notes:

> Once genetic drift has taken place, the chances are that the population in which it has occurred will become extinct, because: (1) the reduction in population which permitted the drift may also have reduced the total number of breeding individuals below the safety level needed for survival; and (2) few genes chosen by chance are likely to be superior to their alternate alleles from the standpoint of survival."(48)

In populations that survive the bottleneck, Coon extrapolates that the process of drift may have sped up the evolutionary process through the speedy fixation of slightly favorable alleles which were normally suppressed by homogenizing gene flow. This interpretation also coincides with the term Coon uses, "The Sewall-Wright effect." This term is clearly drawn from Fisher, who characterized Wright as claiming that such populations were ideal for evolution, although in fact, he claimed it was the large, subdivided population that was ideal (Wright 1948, 1982).

Despite Coon's evident understanding that isolation within a species can promote divergence Coon's still refers back to "mixture" as a source of regional variation, a hold-over from the typological paradigm. Commenting on an ancient origin for "Negroid" features, Coon qualifies the conclusions of the theory by noting; "This theory of the origin of Negroes does not exclude the possibility of mixture between proto-Negroes and Hamits or Capoids. Such mixtures probably took place, and they would explain some of the regional variations among Negroes"(1963:656). The alternative hypothesis, that regional variation does not require mixing of racial types, but simple isolation by distance and random drift, is not even proposed, although he clearly understood the process.

When considering the source of modern humans, Coon surprisingly sounds

pluralistic. He notes in the section entitled, "Was Africa the Cradle of Mankind" that "Darwin considered it to be." And that although "Matthews, Osborn and Andrews shifted attention to Central Asia...now we know human beings (there) were marginal and late" (Coon 1963:656). He also acknowledges that "the cradle was thought to be Southeast Asia, and now Dart, Leaky, Arambourg, and others have again located it in Africa" (Coon 1963:656). He returns however, to his typological, polygenist roots, when discussing the origin of modern *Homo sapiens*, by noting that although Africa was the likeliest origin for *Homo*, "Three of the five human subspecies crossed the sapiens line elsewhere."

If the full context of the "rule" signified by drift had carried over, he would have understood that a large population undergoing regional subdivision could quickly develop racial characters (especially if they were slightly adaptive) and did not require origins stretching back to the speciation of *Homo sapiens.* (In essence, this presumption is carried over into the modern version of polygenism, Multiregional Theory.) Aside from missing the context, Coon also misinterpreted the direction the "random drift" concept was taking. Although he recognized that, "Genetic drift is often invoked to explain differences between species and subspecies....that are of no detectable value in natural selection." (1963:48). He wrongly concluded that; "As our knowledge of genetic processes grows and as our ability to detect survival values increases, we need this theory less and less." (1963:48). Instead, as statistical methodologies have become more widespread, it's been used more and more.

Ironically, another proponent of polygeneist views is Theodosius Dobzhansky. In

his 1963 classic edited by Washburn, Classification and Human Evolution, Dobzhansky distinguishes two distinct models of speciation found in nature, anagenesis and cladogenesis. In the former, species are spread across adaptive landscapes, with different, favorable gene combinations arising in different areas. Subsequently, the populations possessing these superior genes encounter other populations, hybridize to produce even better gene combinations and gradually advance the whole population towards a new equilibrium (Dobzhansky 1963:355). Cladogenesis on the other hand, is identical in its distribution of the adaptive landscape, and differs only in the evolution of reproductive isolation. If the population developing the "superior gene pattern" also develops reproductive isolation, cladogenesis has occurred and the new population will overtake the range of the former (Dobzhansky 1963:355). For Dobzhanksy, the distinction simply boiled down to whether isolation developed or not. In essence the two theories are only separated by historical facts, and not essentially different mechanisms.

Dobzhansky's application of the anagenesis concept to human evolution must be seen in light of this distinction. For his historical facts regarding evolution were coming mainly from Weidenreich (the mentor to Wolpoff, author of the latest version of polygenism, Multiregional Theory) and assumed modern humans appeared only 30,000 years ago. Further, his interpretation of the fossil record was influenced by Weidenreich's firm belief (as mentioned earlier) that racial groups of mankind were not the product of geographic isolation (1946:86). Weidenreich seemingly assumes that the regional differentiations promoted by drift and acted on by selection are in the same category as

large scale structural differentiations that distinguish species. This is not the same manner in which Dobzhansky discusses anagenesis versus cladogenesis. To Dobzhansky, isolation is reproductive and implies a speciation process, not simply the establishment of racial differences. Racial differences are almost certainly established anagenetically within a species. However, to Weidenreich the process that leads to racial differences is conflated into a speciation process by noting that "At least one line leads from *Pithecanthropus* and *Homo soloensis* to the Australian aborigines of today" (Weidenreich 1943a:249-250). While Weidenreich does state that not every Australian can be traced back to *Pithecanthropus*, his misunderstanding of the impact of isolation and drift is nonetheless evident.

Other fields of anthropology, notably archaeology, were also experiencing changes in their paradigm similar to the abandonment of the typological race concept. For archaeologist the shift was initiated by Lewis Binford in his 1965 *Antiquity* article "Archaeological Systematics and the Study of Culture Process." Like Mayr had done for taxonomy in 1942, Binford sought to bring archaeology into the evolutionary fold where it belonged. Binford's comments on drift in this article suggest the cultural "drift" concept has developed biological roots not present in "the disappearance of the useful arts" described earlier by Rivers (1926:200). In the context of "Spatial discontinuities in the distribution of similar formal characteristics" he describes how "drift" was perceived by Ford and Herskovits as a phenomena only evident in "Formal changes in the temporal distribution of items" (Binford 1965:204). Binford's critique of these ideas was aimed primarily at the

"culture center model" that was the basis of the interpretation that deviations in artifacts from a type were necessarily either "innovations" imposed from the center, or "drift" emerging over time. Binford's argument was that culture must be seen as an "extrasomatic adaptation" and hence could vary adaptively over space and time (Binford 1965:205).

For our purposes however, the most interesting aspect of the late-coming Darwinian revolution in archaeology was the degree to which the drift concept was both incorporated and mis-abstracted from biology. The idea that drift would not be evident over space as well as time flatly contradicts the biological definition of drift as it was articulated by Wright. Furthermore, the idea that drift would be evident over time in apparently non-innovational designs ignores the central role drift plays in allowing more "innovational" designs to develop in the first place. While all of these mis-abstractions may derive from a more general mis-abstraction of the biological nature of culture, the exception still proves the rule I quoted from Kuhn earlier. It appears that despite the shared evolutionary paradigm of anthropology and biology, even subdisciplines of anthropology can mis-abstract rules from that paradigm.

During the 1960s, the growing integration of biology and anthropology is reflected in the coupled doubling of research articles on the subject of drift, however, a landmark event was about to occur in 1966 that would spark an explosion in genetic interpretation of human evolution and diversity. In their labs at Berkeley, the biochemists Vincent Sarich and Allan Wilson were examining the rate of fixation of primate genes coding for the production of albumins and yielding results that would soon lead to astonishing

conclusions. With the publication of their article "Quantitative Immunochemistry and the Evolution of Primate Albumins:Micro-Complement Fixation" in *Science*, they established comparative techniques for estimating an "index of dissimilarity" among and between all primates, prosimians and two non-primates (a cow and a pig) that required much less antigen, and was more sensitive to small structural differences in albumin (Sarich and Wilson 1966:1963). The data derived from the index of similarity matched the phylogeny accepted at the time and paved the way for "A large scale survey of species differences in protein structure...with less than a milliliter of antiserum" (Sarich and Wilson 1966:1563).

In anthropology, "genetic drift" becomes increasingly integrated in demographic and ethnographic analysis. Bleibtreu's 1967 article "Some Problems in Physical Anthropology" signifies this growing interest and application of the term. Bleibtreu cites "genetic drift" to explain "genetic differences between adjacent populations considered to be living in identical environments" as well as "a case of marked genetic difference between adjacent and related villages that may be attributed to the maintenance of a founder effect by endogamy" (1967:284). The applications of the drift concept seem valid as the conditions of "Small population size and isolation from other gene pools" are fully outlined as the prerequisites for "random fluctuation in gene frequency" as is the need to rule out "heterozygote advantage" in the rare alleles whose high frequency some interpret as evidence for "random drift" (Bleibtreu 1967:284). Events later that year however, would lead to a vast increase in the application of "random drift" to population dynamics. The event was Sarich and Wilson's 1967 discovery of a "molecular clock" of human evolution.

Chapter 6:

1970s: The Genetics Revolution and the Founding of Molecular Anthropology

When their article, "Immunological Time Scale for Hominid Evolution" was published in the Dec 1967 edition of *Science*, it rocked the paleoanthropology community. Previously, notions of the time scale for the divergence between our hominid ancestors and the ancestors of modern day apes was on the scale from 4 to 30 million years ago. Sarich and Wilson reduced this range to 5-8 million years ago, and subsequently shifted the paradigm of an extremely old history for the origin of modern humans to a relatively recent one (O'Rourke 2003:104). In this context, increased rates of differentiation through random drift and isolation became even more plausible explanations and areas of research. Another aspect of Sarich and Wilson's research which is often overlooked is it's convergence with ideas of neutral evolution proposed by Motoo Kimura two years later (1969). Sarich and Wilson (1967) cite a "steady rate of evolution of albumin" and the recently clear observation that "the structure of proteins closely reflects that of genes" to derive the conclusion that "albumin molecules can serve as an evolutionary clock" (1967: 1200, 1202).

What is often overlooked however, is the sea change in genetics research introduced by their 1966 article in *Science* on "Quantitative Immunochemistry and the Evolution of Primate Albumins: Micro-Complement Fixation" (Sarich and Wilson 1966).

While it not only set the stage for the 1967 article, it also introduced new techniques that made worldwide, increasingly detailed surveys of genetic data a practical possibility by introducing a method that required "much less antigen and antibody is more sensitive to small differences in protein structure...with less than a milliliter of antiserum" (Sarich and Wilson 1966:1563). These technical advances presaged a revolution in the study of human diversity. The statistical approach to population genetics perfected by Fisher and Wright could now be applied to the distribution of human genes on a world wide scale with much greater fidelity. Whereas previously, genes for blood groups were the primary genetic markers employed in genetic research, the wealth of data opened up by Sarich and Wilson meant that the early 1960s "focus of most anthropological genetic studies...to document local patterns of genetic variation within and among populations...to examine the relative effects of evolutionary mechanisms" could now be broadened to reconstruction of ancient population movements and origins (O'Rourke 2003:102).

In the meantime however, Derek Roberts (1968) and L.L. Cavalli-Sforza (1969) were continuing the anthropological research of potential populations "isolates" around the world. Roberts groundbreaking 1968 study on the "historical demography and changing genetic structure of the island of Tristan de Cunha," published in *Nature* and Cavalli-Sforza's 1969 investigation of remote Italian villages in the Alps were both firmly invested in the notion of demographic constraints on genetic variation resulting from drift (O'Rourke 2003:102). These early investigations, at least in Cavalli-Sforza's case, were continuations of ideas derived from Fisher (whom Cavalli-Sforza trained with in

Cambridge after receiving his PhD). In Cavalli-Sforza's 1966 article "Population Structure and Human Evolution" he outlines his rationale for studying the effect of drift on remote populations. First he theorizes that man is an ideal subject for this approach, since demographic records are more evident than for other species; second, Cavalli-Sforza concludes that although "temporal variation in selective coefficients" will simulate drift (randomly varying selection - a clear import from Wright), a steady change affecting all alleles will be an equally clear indication of drift (Cavalli-Sforza 1966:364).

Cavalli-Sforza is clearly considering selective forces at this point, mainly as a result of his training as a geneticist and as a statistical biologist under Sir R.A. Fisher. However, as Cavalli-Sforza delves more into anthropology, and the scope of his studies broaden into reconstructing greater and greater times scales and population shifts, the application of the drift concept is extended to entire populations far removed from the constraints recognized by Wright and Fisher. This transition is best evidenced in the Huxley memorial lecture Cavalli-Sforza gave in 1972, published later in the *Proceedings of the Royal Anthropological Institute* as "Origin and Differentation of Human Races" (1972). In this article, Cavalli-Sforza outlines the interplay between selection, drift, migration, and isolation and even cites Lewontin's 1972 calculations of the F value (a statistical measure of genetic distance) which indicated that random drift alone cannot account for the genetic distance between human geographic races (1972:17).

However, Cavalli-Sforza's balanced description of the interdependency of selection and random forces is not as noteworthy as his statistical correlation between the steady

divergence accumulated through random drift and the time since such divergence began. From his previous studies of isolated alpine villages, which he acknowledges as the only suitable conditions for fully distinguishing impact of drift, entire geographic races are now considered subject to drift. Cavalli-Sforza (1972:17) proceeds with the extension of the drift concept, although he realizes, "When comparing racial groups that occupy virtually the whole world...selection conditions... vary considerably" and that estimates of time based on the simple drift formula are "not possible."

For Cavalli-Sforza, these challenges are overcome by introducing a "time yardstick for separations that have been dated by archaeological means" which provides "estimate rates of evolutionary divergence" (1972:17). This estimate, drawn from the assumption that Native Americans entered the new world "between 10,000 and 25,000 years ago" is then suggested to be "not inconsistent with the notion that modern man appeared on the world scene, as judged from skeletal remains, at least 50,000 years ago" (Cavalli-Sforza 1972:17-18). The notion of genetic drift, once absent from early reconstructions of human evolution, has now become the central concept underlying reconstructions of the modern human family tree. As Cavalli-Sforza noted when it was introduced:

> Reconstruction of trees of descent is satisfactory if certain postulates are met...We cannot yet be certain that such postulates are fully satisfied...The major postulate is that the measurement of genetic distance employed is proportional to separation time. This can be more easily achieved if the major source of differentiation is random (1972:20).

The major constraint on the substantially broadened application of drift is the degree to

which the frequency of genetic polymorphisms is independent of environmental factors. Other discoveries were also acting in concert to reinforce the emerging rule that "random drift" was widespread through out the genotypes of animal species and hence a reliable "molecular clock."

In other areas however, notably Birdsell's 1972 textbook Human Evolution, we see a more restrained definition of drift. In this instance, although "random drift" is actually conjoined with the founder principle into "founder drift," the definition is surprisingly thorough and accurate (Birdsell 1972:412). Birdsell cites Dobzhansky's experiments on fruit flies, which indicate the precise balance between selection and population size, and provides empirical examples of population sizes in Australian aboriginal groups that are candidates for drift (40-50), and sums the relationship up nicely as "Drift pulls the trigger and selective forces then come into action to create a new level of equilibrium in the gene pool" (Birdsell 1972:407,413-14). Most importantly, Birdsell comments on the distribution of blood groups and disease resistance, and the impact for interpretation of drift at the scale employed by Cavalli-Sforza presented fresh evidence that malaria resistance through the sickle cell gene is an example of selection for a balanced polymorphism, and that the distribution of blood groups in the New World is "under selective control since it cannot be presumed to have originated through massive gene flow. The fact that clinal surfaces are quite regular gives no other possible explanation" (Birdsell 1972:407). While Birdsell acknowledges that disease resistance seemed an unlikely explanation for the smooth clinal surfaces at the time, he concluded nonetheless that

smooth clinal surfaces, as they were for other adaptive features, were a "smoking gun" for selection. For Birdsell at least, the "shared paradigm" is evident at this point.

The transition to the wider scope of the drift concept initiated by Cavalli-Sforza is shown most clearly in the textbooks that follow Birdsell's 1972 edition. In Philip Stein and Bruce Rowes' 1978 edition of <u>Physical Anthropology</u> for example, "genetic drift" is defined as "sampling error" represented in the "chance deviation in the frequency of alleles in a population" and the "founder principle" is equated as "another form of sampling error" (1978:101). This suggests the further extension of drift into "colonization, trade, exploration" with the specific examples of the H.M.S. Bounty mutineer's founding of Pitcairn island, and the endogamous Amish of Lancaster County, as instances of "the founder effect, genetic drift, and consanguineous mating" since "in this population is found fairly high frequencies of some rather rare alleles" (Stein and Rowe 1978:105).

While it is true that the process of random drift can certainly explain high frequencies of rare alleles, the important distinction that has been lost in these is the evolutionary significance of the process as it relates to natural selection. In addition, the former distinction, maintained by Mayr (1963) that random drift and the founder principle should be separate concepts since they imply different demographic events, has been lost. This trend towards conflating "founder effect" and "random drift" is also evident in the research articles of the time, such as Neel and Thompson's "Founder Effect in Tribal Population"(1978). Neel and Thompson provide a new definition of "founder effect," based solely on genetics, that is conflated with the distinct concept of "genetic drift":

> When an unusually high frequency of an allele is encountered in a population, "founder effect" is often invoked as an explanation. As usually used, the term implies the disproportionate increase through chance (rather than selection) of an allele (1978:1442).

No longer are the strict guidelines of a population founded by a "single breeding pair" or "fertilized female" (Mayr 1942) used, but virtually any situation in which endogamous breeding has occurred fits the new criteria. Also, the fundamental link between drift and selection as a source and cause of variation is lost. This loss of the "directedness" aspect of genetic drift and the founder effect is most evident in another article by Neel and Thompson (1978) where the variation in 25 proteins found in 12 Amerindian tribes over a twelve year period is interpreted under the "assumption that the phenotypes in question are selectively neutral" (1978:1904). Whether the assumption is valid is irrelevant because the new definition obviously does not require it. The null hypothesis has shifted from selection to randomness as the main factor determining phenotypes.

Chapter 7

1980s-1990s: Eve and the Haplotype Tree of Knowledge

The 1980s see a continuation in this trend. The most significant event was Matoshi Nei's and A. Roychoudhury's (1982) publishing of an evolutionary tree based on the frequency of different protein-coding alleles detected by electrophoresis, and blood group loci. This tree suggested an early modern human radiation from Africa around 110,000 years ago, followed by a second radiation nearly 41,000 years ago (Nei and Roychoudhury:1982). During this period molecular anthropology also developed the statistical complexity and technical ability to address questions of mitochondrial divergence. The early data from Nei and Roychoudhury, which suggested an early origin for modern man in Africa, could potentially be reinforced if the data supporting a mitochondrial DNA (mtDNA) model of human evolution and dispersal could be obtained and validated. In 1987, Cann, Stoneking and Wilson accomplished this feat, and published the first haplotype tree of human mtDNA along with their estimates that it reflected a human population in Africa between 140,000 and 290,000 years ago (Cann et al 1987:31).

Underlying this estimate was the assumption that the "molecular clock" analogy was even more accurate for mtDNA, since its direct transmission from mother to daughter rendered it supposedly immune from selection and recombination. Hence, the only factor affecting mtDNA variation was the steady accumulation of mutations (at a rate of 2-4 percent divergence per million yrs), a much easier estimate than "genetic drift" (Wainscoat 1987:13). However, "genetic drift" was not completely ruled out by the critics of the early

versions of the mtDNA tree. For although the passage of mtDNA without recombination ensured "sampling error" was avoided during sexual meiosis, "sampling error" at the level of populations was not.

This point was cited by Wainscoat as an alternative explanation for the data, "that one ancestral mitochondrial DNA type has reached fixation by random genetic drift" making it possible that "the date of the mitochondrial Eve is associated with the most recent population bottleneck" (1987:13). These distinctions also reveal the state of the "genetic drift" concept in light of mtDNA research. Since "genetic drift" may complicate mtDNA analysis, its known association with bottlenecks is assumed the most parsimonious explanation. Thus, rather than address the complicating factors which would also apply to application of the "random drift" concept itself (the bottlenecks may have resulted from disease, or similar selective pressures), the initial constraints on random drift have become "twice removed" from the argument.

As mentioned earlier Mayr (1963: 204, 534) does not consider the "founder effect" to be a case of random drift, and like Wright, considered selection to be the ultimate guiding force, (Beatty, 1999) yet this distinction has been completely lost in most cases by the 1990s. This is the first major disjuncture between biology and anthropology of the 1990s, for research continues into the role of the founder effect on speciation at this point, and distinctions continue to be drawn between the two. An illustration of a mis-interpretation of "drift" and "isolation" can be found in Milford Wolpoff's "center and edge" metaphor underlying his alternative to the "Out of Africa Model," the Multiregional

Model of human evolution (1988). In the 1997 book, Race and Human Evolution, Wolpoff and Caspari outlines some key concepts, and identifies their intellectual forbearers. However, the manner in which their ideas are applied suggest a significant mis-abstraction of the rules derived from Wright's calculations. Wolpoff and Caspari's concept of the relationship between variation within and between subpopulations is defined as:

> Populations in the center should be heterogeneous because selection weeding out variations should be less intense where humans are best adapted. Furthermore with denser habitation more populations were in contact, leading to more genetic exchanges and variation (Wolpoff and Caspari 1997:264-5).

This "center" as applied by Wolpoff and Caspari, is Sub-Saharan Africa. Hence the consequences they derive from this assumption are that higher genetic variation in Africa is solely the result of larger population size and greater gene exchange. They then derive that time depth should be not seen as a factor in this interpretation, because they interpret "less variation" on the periphery as an indicative of populations isolated by distance (Wolpoff and Caspari 1997: 265-7).

This conclusion is highly divergent from Wright's 1982 comments on the occupancy of new ecological niches in which he reemphasized that "speciation may come first, because of geographical isolation of a portion of the species" (441-442). Wright's assertion is not only that isolation on the periphery would inevitably lead to divergence, but such divergence is a direct consequence of the fact that large, panmictic populations have stabilizing gene flow for polymorphisms, and are hence, homogenous with respect to peripheral populations (Wright 1982:434). The dissimilarities between "center and edge"

and Wright's models of speciation within large, subdivided populations are most apparent in Wright's own description of the process of speciation at the moment a new adaptive pattern arises:

> There must, however, be enough diffusion that a deme that happens to acquire a favorable interaction system may transform its neighbors to the point of autonomous establishment of the same peak, and thus ultimately transform the whole species or at least that portion of it in which the new system actually is favorable (Wright 1982:435).

In Wright's own description, the most likely "transformation" of a species will be at the very "edge" Wolpoff and Caspari identifies as effectively stagnant-having less heterogeneity that the center. Furthermore, while the whole species may be transformed by the new adaptive pressure, there is a good chance speciation may happen first in the geographically isolated portion of the population. Wright's own remarks for the application of this concept to living species also suggests that his interpretation of the concept of genetic drift and Wolpoff and Caspari's have diverged. Wright notes that "there are many cases in which a chain of intergrading subspecies has returned on itself in a circle and it is found that the overlapping populations coexist without interbreeding" (1982:438).

This fundamental interaction between reproductive isolation (speciation) and geographic isolation was a common observation made by Wright (in the lab) and Mayr (in the field) and is the central premise of their concepts of "genetic drift" and the "founder principle." For Wolpoff however, this paradigm does not appear to be completely shared, as Wolpoff and Caspari note in Race and Human Evolution (1997) that Wolpoff's

reinterpretation of "evolutionary continuity in Europe as a consequence of genic exchange balanced with selection and drift, not a consequence of isolation as he had thought" represented a "shifting evolutionary paradigm" (269). I would contend however, that Wolpoff still shares the evolutionary paradigm, but has simply mis-abstracted a rule from it. Otherwise, he would acknowledge that the "center and edge" metaphor does not correspond to "the idea of an adaptive landscape" which he derives "...from the work of Sewall-Wright" (Wolpoff and Caspari 1997:293).

The mis-abstractions are also evident in the interpretations of the selective topography of the "adaptive landscape." Wright emphasized that adaptations were "peaks" which indicated difficulty in ascending, since they are separated not only by differing selective pressures, but by the "valleys" which represent "pleiotropic effects" that act to maintain successful gene complexes (1982:431-432). Wright's topography thus emphasizes that peak shifts (which move successful gene complexes around the landscape) are difficult and require special conditions. Wolpoff and Caspari on the other hand, claim that "the idea of stable configurations is better expressed by dips" and that "Species, or geographic races within them, have gene pools with frequencies that gravitate toward these stable adaptive valleys" (Wolpoff and Caspari 1997:295). This interpretation completely ignores the "random wandering" about the adaptive peak that Wright claims typifies populations subject to "genetic drift" or the "founder effect." This process was central to Wright's model, since it demonstrated the "trial and error mechanism by which in time the species may work its way to the highest peak in the general field" (Wright 1982:434-435).

Thus Wolpoff and Caspari's interpretation of "valleys" suggests that change is inevitably towards the fixation of local adaptations, without the evolution of local reproductive isolation. For Wright, the development of reproductive isolation is a direct consequence of the nonadaptive random divergence of gene frequencies that accompanies isolation and smaller population size on an adaptive peak. However, Wolpoff and Caspari's interpretation leads them to conclude the opposite, that "One of the best arguments for a significant European Neandertal input into the gene pools of later Europeans is the persistence of nonadaptive traits" (1997:296). While Wolpoff and Caspari correctly assert that "Nonadaptive features can persist after they are established at high frequency," they wrongly concludes that they can only be interpreted as a lineage, when they may simply be the result of random variation being repeatedly fixed in small subsequent populations.

CONCLUSION:

2000: A Return to the Founding Definition.

This thesis has sought to demonstrate that the existence of a shared evolutionary paradigm does not automatically guarantee the existence of shared rules abstracted from that paradigm. The process of abstraction, fundamentally a "sampling" of ideas from within a *meme* pool, can potentially result in divergence of rules. When concepts such as drift and the founder effect, are separated from the *meme* pool, they become open to reinterpretation in accordance with earlier, often inappropriate, paradigms. They are also cut off from the larger community of ideas (or *memes*) which could potentially stabilize them. In the example discussed above, Wolpoff and Caspari's earlier remark that Wolpoff's evolutionary paradigm "shifted" is an instructive example of the dangers inherent in isolation. From this initial shift, the Multiregional Model has been like a castle built upon the sand. Without the foundation of a mutually criticized set of shared rules derived from the evolutionary paradigm, numerous models can come to represent little of the variation we truly see in nature.

There is also the more subtle, and dangerous pattern of previous paradigms continuing to exert influence, despite the shared evolutionary paradigm. This pattern has been demonstrated with the early 20th century notions of race and its effects on the idea of random drift as a function of isolation. The concept of race as an essential quality inhibited the standardization of the geographical race concept, and hence the role of random drift, isolation, and the founder effect played in establishing racial diversity was misunderstood

by well-known anthropologists (Coon 1963, Garn 1955) even into the 1960s. Subsequently, the emergence of molecular genetics during the 1960s shifted the scope of genetic drift from small isolated populations, to entire species. Accompanying this shift, was a dramatic reinterpretation of the timescale of hominid evolution, which further reinforced the utility of the "genetic drift" concept as it applied to species.

While research in biology continued to investigate the probability of speciation via genetic drift versus selection, anthropologists and geneticists (Neel and Thompson 1978, Cavalli-Sforza 1972) were rapidly applying the "genetic drift" concept to reconstructions of founding events in human demography during the Pleistocene. This trend (in biology and anthropology) has prompted Mayr (2000) to reiterate the issue of scale in reconstructions of the "founder effect" as "The fate of peripherally isolated populations is often very different as they are usually founded by a *small number* of individuals, indeed often by a *single* fertilized female, and contain only a small fraction of the total genetic variability of the past species" (emphasis added) (602). While in some instances, the key conditions for establishing a potential "founder population," isolation and extremely small population size, almost certainly existed on a wide scale during the Pleistocene. Mayr insists that despite the conditions for drift existing, selection is nonetheless "...the real cause of genetic changes occurring in a founder population" and is the most instructive interpretation for understanding not only the rise of modern humans, but also their differentiation (1998: 445).

The most recent research (Apr 2003), by Sean Carroll (a geneticist investigating the

genetic basis of the traits that distinguish humans from primates), suggests that Mayr may be more right than he realizes. Rather than completely rule out selections role in patterning the variation seen in modern human genotypes, Carroll suggests that the concepts of randomness and direction must be combined under one rubric, "Selective Sweeps" wherein "selection may drive the allele bearing that change to fixation...In the process, neutral variation at linked sites 'hitchhikes" along with the selected site" (Carroll 2003:854). In Carroll's groundbreaking application of linkage analysis to formerly "neutral alleles" the scope with which selection may act has once again shifted the debate back to the original observations made by Gulick, Wright, Mayr, Dobzhanksy, and Birdsell. Rather than apply on the broadest possible scale an abstraction of one aspect of the evolutionary paradigm (genetic drift/founder effect), both aspects (randomness and direction), should be re-integrated into genetic drift and founder effect concepts.

Appendix I:

I **Biological Journals Reviewed:**

Found under JSTOR section: "Ecology"
American Midland Naturalist 1909-1999
Midland Naturalist 1909
American Naturalist 1867-1998
Annual Review of Ecology and Systematics 1970-1997
Biotropica 1969-1997
Conservation Biology 1987-1999
Diversity and Distributions 1998-1999
Biodiversity Letters 1993-1996
Ecological Applications 1991-1998
Ecological Monographs 1931-1998
Ecology 1920-1998
Evolution 1947-1999
Functional Ecology 1987-1999
Global Ecology and Biogeography 1999
Global Ecology and Biogeography Letters 1991-1998
Journal of Animal Ecology 1932-1999
Journal of Applied Ecology 1964-1999
Journal of Biogeography 1974-1999
Journal of Ecology 1913-1999
Journal of Tropical Ecology 1985-1997
Limnology and Oceanography 1956-1999
Paleobiology 1975-1998
Quarterly Review of Biology 1926-2001
Systematic Biology 1992-1999
Systematic Zoology 1952-1991

Found under JSTOR section: "General Science"
Philosophical Transactions: Biological Sciences 1990-1997
Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences 1934-1990
Philosophical Transactions of the Royal Society of London. Series B, Containing Papers of a Biological Character
1896-1934
Philosophical Transactions of the Royal Society of London. B 1887-1895
Philosophical Transactions of the Royal Society of London 1776-1886
Philosophical Transactions (1683-1775) 1683-1775
Philosophical Transactions (1665-1678) 1665-1678
Philosophical Transactions: Mathematical, Physical and Engineering Sciences 1996-1997
Philosophical Transactions: Physical Sciences and Engineering 1990-1995
Philosophical Transactions of the Royal Society of London. Series A, Mathematical and Physical Sciences 1934-1990
Philosophical Transactions of the Royal Society of London. Series A, Containing Papers of a Mathematical or
Physical Character 1896-1934
Philosophical Transactions of the Royal Society of London. A 1887-1895

Philosophical Transactions of the Royal Society of London 1776-1886
Philosophical Transactions (1683-1775) 1683-1775
Philosophical Transactions (1665-1678) 1665-1678
Proceedings: Biological Sciences 1990-1997
Proceedings of the Royal Society of London. Series B, Biological Sciences 1934-1990
Proceedings of the Royal Society of London. Series B, Containing Papers of a Biological Character 1905-1934
Proceedings of the Royal Society of London 1854-1905
Abstracts of the Papers Communicated to the Royal Society of London 1843-1854
Abstracts of the Papers Printed in the Philosophical Transactions of the Royal Society of London 1800-1843
Proceedings: Mathematical, Physical and Engineering Sciences 1996-1997
Proceedings: Mathematical and Physical Sciences 1990-1995
Proceedings of the Royal Society of London. Series A, Mathematical and Physical Sciences 1934-1990
Proceedings of the Royal Society of London. Series A, Containing Papers of a Mathematical and Physical Character
1905-1934
Proceedings of the Royal Society of London 1854-1905
Abstracts of the Papers Communicated to the Royal Society of London 1843-1854
Abstracts of the Papers Printed in the Philosophical Transactions of the Royal Society of London 1800-1843
Proceedings of the National Academy of Sciences of the United States of America 1915-2000
Science 1880-1997
Scientific Monthly 1915-1957

Appendix II:

[II] **Anthropological Journals Reviewed:**

Found under JSTOR section: "Anthropology"
American Anthropologist 1888-1995
Transactions of the Anthropological Society of Washington 1879-1885
American Antiquity 1935-1997
American Ethnologist 1974-1995
Annual Review of Anthropology 1972-1997
Biennial Review of Anthropology 1959-1971
Anthropology Today 1985-1997
RAIN 1974-1984
Cultural Anthropology 1986-1995
Current Anthropology 1959-1999
Yearbook of Anthropology 1955
Ethnohistory 1954-1999 (plus links to recent content 2000-2002)
Ethos 1973-1995
Journal of American Folklore 1888-1997
Journal of the Royal Anthropological Institute 1995-1997
Man 1901-1994
Journal of the Royal Anthropological Institute of Great Britain and Ireland 1907-1965
Journal of the Anthropological Institute of Great Britain and Ireland 1872-1906
Medical Anthropology Quarterly 1983-1995
Medical Anthropology Newsletter 1968-1982
Proceedings of the Royal Anthropological Institute of Great Britain and Ireland 1965-1973

Appendix III:

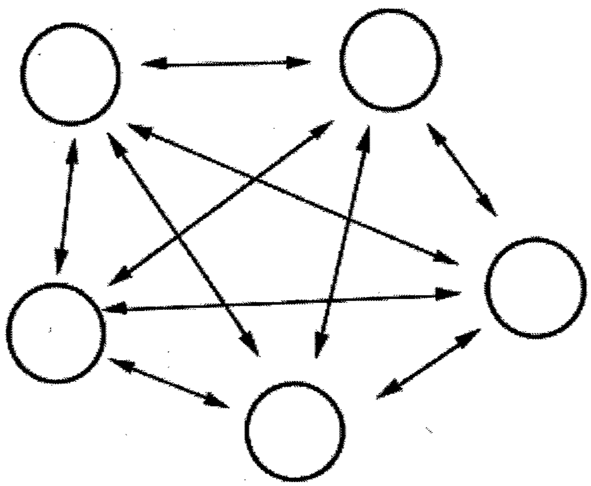
[III] The first eight presidents of the American Association of Physical Anthropologists were:
Ales Hrdlicka (1930-1931)
Adolph H. Schultz (1932-1934)
Raymond Pearl (1934-1936)
Earnest A. Hooton (1936-1938)
T. Wingate Todd (1938)
Raymond J. Terry (1939-1941)
William K. Gregory (1941-1943)
Charles B. Davenport (1943-1944)

From American Association of Physical Anthropologists website: www.physanth.org/pastpres.html

Appendix IV:

IV From Michael C Whitlock and David E Mccauley, "Indirect measures of gene flow and migration: F_{ST}¹1/(4Nm+1)" in *Nature*. February 1999, Volume 82, Number 2, Pages 117-125:

Wright's 1931 calculations described the "Island Model" which underlies the theory of genetic drift. Graphically, this model is most succinctly represented thus:



The island model. Each population receives and gives migrants to each of the other populations at the same rate *m*. Each population is also composed of the same number of individuals, *N*.

Wright's other mathematical contribution in 1931 was *F*-statistics, a set of hierarchical measures of the correlations of alleles within individuals and within populations. The *F*-statistic most relevant to the study of gene flow is F_{ST}, which has various interpretations; most famously it is the variance in allele frequencies among populations, σ^2_p, standardized by the mean allele frequency (p) at that locus:

$$F_{ST} = \sigma_p^2/[p(1-p)].$$

Wright predicted a simple relationship between the number of migrants a population receives per generation and F_{ST}. Under the assumptions of the island model,

$$F_{ST} \approx 1/(4Nm+1),$$

where N is the effective population size of each population and m is the migration rate between populations. Advances in molecular techniques have allowed direct estimates of F_{st} and hence promise increasingly accurate measurements of migration rates. A demographic application not overlooked by anthropologists during the sixties and seventies.

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